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UNUSUAL MODES OF BREEDING AND DEVELOPMENT AMONG ANURA.

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IT has been my good fortune to obtain from Jamaica a complete series of stages of the development of *Hylodes martinicensis*. The eggs of this frog are deposited on land, and the entire development takes place within the egg-membranes. The stages that correspond to the tadpole of our common frogs are passed through inside the egg-membrane and a fully formed frog emerges at the time of hatching. In connection with the study of the development of Hylodes it has been necessary to collect the descriptions that have been given of exceptional modes of development in the Anura. These accounts are often very fragmentary and widely scattered, so that no small labor has been necessary to bring together the literature of the subject. In the hope that a consecutive and full account of what is known may be of service to others, the following pages have been prepared.

In the groups of fishes and Amphibia the eggs are generally laid in large quantities and are left unprotected, but there are other exceptional modes of propagation in species of

unrelated genera and families. In these cases protection of some sort is generally afforded to the young, or else they have become adapted to an unusual environment. As a result, modifications in the young have been produced, as well as changes in the instincts and even in the anatomy of the parents. Examples among fish are the various cases of nest builders among teleosts; the cases of Bagrus, of the siluroid Chromis, and of other fish that carry the young in the mouth for a longer or shorter period; the case of *Aspredo lævis*, in which the female carries the eggs and young attached to pedicels on the abdomen; the cases where the male fish is provided with a temporary or permanent pouch for the young, and the cases of partially or entirely viviparous forms among teleosts and selachians. Examples among Amphibia are the viviparous salamander; Plethodon and Autodax, which lay their eggs on land; Desmognathus, Amphiuma, and the Cœcilia, where the eggs are laid in damp places and are surrounded by the parent's body; and a number of Anura, which are the subject of the present paper. For the sake of comparison with what is to follow, the salient points in the development of the common frog may be briefly stated. The eggs are laid in large numbers in water, where the larvæ develop. The newly hatched tadpole adheres at first to a fixed object by means of an adhesive gland, but after a few days it becomes free-swimming. It possesses at first external gills; these are replaced by internal gills, covered by the characteristic operculum; the internal gills are in turn gradually replaced by lungs; in the mean time the hind legs and later the fore legs develop; the tail is absorbed, the shape and position of the mouth are changed, the larval "mouth-parts" are cast off, and the characteristically coiled intestine is shortened. The metamorphosis transforms the aquatic larva into the adult air-breathing form.

This general account is true for all the common frogs and toads of North America and Europe, with the exception of Alytes. The Anura of other regions, especially in the Tropics and the Southern Hemisphere, far from having uniform breeding habits and one mode of development, vary

in many ways. For the sake of completeness, a number of forms will be mentioned that are often referred to in connection with those that have an unusual mode of development; they are forms whose embryology has been but little, if at all, investigated, but whose development takes place under somewhat unusual conditions, so that the embryology is a question of interest.[1]

The eggs of the Japanese frog, *Rhacophorus schlegelii*, are laid from the middle of April to the middle of May in excavations prepared by the female in the muddy banks of paddy-fields, ponds, lakes, etc., 10 to 15 cm. above the water line. As the eggs are laid, they are fertilized, and the gelatinous substance about them is aërated by a kneading motion of the hind legs of the female. Both adults usually escape from the nest by breaking a hole in the side of the bank exposed to the water. The frothy egg-mass hardens on the outside, and within it the tadpoles hatch. The substance about the eggs gradually collapses, and in time flows into the water, carrying with it the tadpoles. The eggs are about 1 mm. in diameter, and devoid of pigment until the tadpole stage, when pigment begins to show in the pectoral region. The segmentation is said to be unequal and holoblastic, though more nearly meroblastic than in any other amphibian egg.[2] The embryo is described as resembling a ganoid embryo, the head being flat upon the yolk, and the body wedged into the large yolk-mass.

It is interesting to note that eggs taken from the nest in the mud invariably die if put into water.

Eggs that are said also to be those of Rhacophorus have been found in various localities in Japan, in a frothy, gelatinous substance on the leaves of trees overhanging the water. How the eggs are deposited is not explained.

Two other frogs, from different parts of the world, leave their spawn on trees, in nests formed of leaves stuck together. One of these, the West-African *Chiromantis guineensis*, is found

[1] For an index to the forms discussed, with summary of literature referring to each, see Appendix, p. 714. References to reviews are given after special articles.

[2] The segmentation of several other anuran eggs that contain much yolk has not as yet been described.

in Cameruns, Victoria; the other, *Phyllomedusa iheringii*, in the province of Rio Grande, Brazil. In both cases hatched tadpoles have been seen, moving with considerable freedom, in the frothy mass in which the eggs are laid. The nest of the Phyllomedusa has an inferior opening over the water. It is believed that the tadpoles of Chiromantis are washed off the leaves by rain. Tadpoles, hatched in confinement, at first swam in the gelatinous substance which liquefied about them, and being transferred to water, they lived and developed. The account of Chiromantis opens with an exclamation on the remarkable character of the metamorphosis of the frog, and yet the tadpoles are described as having a "rudder-tail, a clump of gills, etc., just like an ordinary tadpole," and they "developed (in water) in the usual way."

The little *Phyllomedusa hypochondrialis*, in Paraguay, selects for the deposition of its eggs a single leaf on a plant near a pool, or over it, not more than two feet above the water. The female carries the male, until a suitable leaf is found; then both frogs hold the tip of the leaf together with their hind legs, and in the funnel thus formed the eggs are deposited, the frogs moving up the leaf as the bottom is filled. One pair of frogs may make two nests with about 100 eggs in each. The eggs contain much yolk and measure 2 mm. in diameter. If put into water, the eggs die, but develop if they are simply kept moist. The tadpoles hatch and escape from the leaf into the water after six days; if the nest has not been directly over the pool, the tadpoles may move (assisted by a jumping motion) several inches along the ground during a shower.

Segmentation is holoblastic, but not very regular; the blastopore closes and a new anus is formed. The embryo at first lies flat upon the yolk, but before the yolk is absorbed the embryo is modeled high up upon it, and the head and tail are entirely separate from it. The yolk is covered by a plexus of vitelline veins.

Three visceral pouches, the 1st, 2d, and 3d branchial, are formed, and external gills appear first on the 1st branchial arch and later on the 2d. The first pair grow rapidly and soon become very long, branched filaments; the second pair

never develop to the same extent. No adhesive gland is formed. When the external gills are developed the tail has grown to a large size and has so ample a blood supply from the dorsal aorta and cutaneous veins that it is supposed to be an important organ of respiration. After hatching, the tip of the tail often vibrates rapidly, perhaps to insure the flow of a constant stream of water over the tail.

Before hatching, the operculum grows back from the hyoid arch, and has a median spiraculum; the external gills are rapidly absorbed, and internal gills are developed. The stomodæum breaks through, at the last stage in the egg, and the tadpole hatches as a free-swimming, transparent larva, with prominent eyes, and with no longer any trace of yolk. The lungs are present. On the day after hatching, pigment appears in the larva.

Five weeks later the hind legs begin to develop, and the tail is absorbed very rapidly, until only a little of it remains. After the legs are formed the frog leaves the water, and the final absorption of the tail takes place on land.[1]

The eggs of *Hyla nebulosa*, found in Rio de Janeiro, hatch in a frothy mass in the sheath of withered banana leaves, but not near a pool. Unlike the tadpoles of Chiromantis, which probably reach the water in the natural course of events, the tadpoles of *Hyla nebulosa* invariably die if they are transferred to water.

The tadpoles of *Cystignathus* (*Paludicola*) *gracilis* in Brazil, and of a frog believed to be *Rhacophorus eques* in Ceylon, are said to undergo part, at least, of their development out of water. The eggs have been found in frothy masses on land, those of Cystignathus usually in the grass in the neighborhood of pools. The adult Cystignathus, and on one occasion two young, were found under decaying trunks of trees, near dried ponds; the larger of the two young possessed the vestige of a tail. The naturalist d'Orbigny found the same species in the Argentine Republic, where it occurs under pieces of wood, near the borders of lakes that are common in the sandy soil. The tadpoles of Rhacophorus were observed superficially and are said to resemble those of the ordinary frog.

[1] For further details, see Budgett ('99).

The adult of the Brazilian frog, *Cystignathus mystaceus*, in the province of Rio Grande do Sul, never goes to water, even to spawn. In the breeding season it prepares a hole under a stone or decayed wood, near the edge of a pool, but above the water line; here the eggs are deposited in comparatively small numbers. The frothy substance about them probably serves as food for the tadpoles, since it diminishes in quantity as they grow. In a dry season the tadpoles may attain great size in the nest, but ordinarily they are washed into the pool, when, after a rain, it overflows. They probably do not go through the entire metamorphosis in the nest, however long they may be detained in it, for tadpoles that had grown there to a considerable size still possessed tails. During development in the nest, external gills were observed; the tail was thought to be not so powerful as that of *Rana esculenta*, and is at first light in color, like the egg, but later becomes pigmented dorsally. Another Brazilian nest builder is *Hyla faber*, which is common in Rio de Janeiro, especially in the mountain regions. The female constructs for the eggs a shallow vessel of mud, about four inches high and a foot in diameter. The nest is carefully built on the bottom of a pool, with its edge projecting above the water. Similar nests have been found in Rio Grande do Sul,[1] and there it has been observed that, if the pool dries, the tadpoles in their little lagoons perish, while the young of *Cystignathus mystaceus* survive, huddled together in the frothy substance in their nest in the bank. The eggs of *Cystignathus typhonius*, a frog common in Porto Rico, have been found under conditions similar to those described in the case of *C. mystaceus*. The tadpoles swam when put into water. The appearance of the hind legs and of the fore legs and the disappearance of the tail were observed.

In Ceylon, a green frothy spawn, about the size of a crow's egg, has been found sticking to the walls of cisterns, to perpendicular rocks of quarries over water, and to the damp

[1] It was formerly supposed by the observer in Rio Grande do Sul that such nests were constructed by *Cystignathus ocellatus*, but there is good reason to suppose that *Hyla faber* is the artisan. In Rio de Janeiro this frog has been observed in the very act of building, which takes place at night.

trunks of trees. After some discussion it has been decided that the spawn is that of *Polypedates maculatus*. A very similar account is given of the blue spawn of *Rana temporalis*, also found in Ceylon. The two descriptions agree so closely that one is led to suspect that the two cases may be one and the same.

The tadpoles of a Brazilian frog, *Hyla* (*Ololygon*) *abbreviata*, have been found in cracks of rocks. The abdomen of the tadpole is flat and serves as a sucker, so that if the perpendicular rock is slightly moist, the tadpole can move rapidly over it without legs. The tail is round, with a fin only at the end; on the ventral side the fin is anteriorly converted into a sole, which probably aids the tadpole in adhering to the rock. The mouth is large and the lips are unusually developed. It is said that the frogs, for a time after metamorphosis, are the color of the rocks. Nothing is recorded as to where the eggs are laid, or how they develop.

The breeding habits of *Pipa americana*,[1] commonly known as the "Surinam toad," have been a subject of observation, still more of discussion, from time to time for more than a century. It has been found in British as well as in Dutch Guiana. The frogs are said to be essentially aquatic, and rarely to leave the water. The eggs are laid in the dry season, when the temperature is exceedingly high. The earlier accounts of spawning are probably based on the observations made by Fermin in Surinam, and published in 1765. He states that the eggs are laid on the sand and are placed by the male on the back of the female; a few minutes after fertilization the female returns with them to the water and swims off. The spawning has recently been described in a different way, as observed on one occasion in the Zoölogical Gardens of London. The animals remained in the water, the oviduct was protruded into a bladder-like pouch, turned up over the back; the male clasped the female, and pushed the eggs out of the bladder, leaving them evenly distributed over the back of the female. It is supposed that the eggs are fertilized in the ovipositor.

[1] A few embryos of Pipa have been in the possession of the Warren Anatomical Museum of the Harvard Medical School.

The dorsal skin of the female thickens about the eggs, until each is enclosed in a dermal "cell" or sac, which is finally covered by an "operculum." Leydig ('96) regards the cells as modified glands, and, in corroboration of his view, states that other dermal glands are not found where the cells are formed; he regards the cap of the cell as a secretion of the gland, while formerly it was thought to be a hardened portion of the gelatinous substance around the egg. Whatever the origin of the cells, they are temporary structures which form in response to the stimulus of the eggs; the number of eggs carried by one frog has been variously estimated, and may be more than one hundred.

The eggs develop entirely within the dermal cells, and Fermin has observed that they remain about eighty-two days on the back of the parent. I have found no direct statement as to whether the time of hatching is coincident with the time of leaving the dermal sac, except in Bronn's Thierreich. There it is said that "the hatched young find shelter and nourishment on the parent's back, until after completed metamorphosis," implying that the eggs are hatched some time before the young escape.

The only description of development, based on the observation of many embryos, is one by Jeffries Wyman ('54), giving the external characters of three stages.

The limbs develop early; even in the youngest stage, where there were three pairs of external gills, the fore and hind legs were present, in the condition of knobs at the sides of the embryo, the posterior said to be unconnected with the trunk. There were at this stage vitelline vessels, supplying the large yolk-mass. The head was broad and flat, with conspicuous cerebral vesicles and prominent pigmented eyes; the spinal cord was closed.

Later (in the second stage), when the external gills had disappeared, fringed branchial arches were seen by removing the dermal folds which concealed them; the opercular folds opened by a small branchial fissure on each side of the neck, and judging from the figures, did not cover the anterior legs. Rudiments of feet were present on all the extremities. It is

said that the whole yolk-mass was invested with a "tunic" and converted into a spiral intestine, returning to the trunk through the middle of the coil! The nostrils in this stage were seen as round terminal depressions.

In the last stage toes were formed; the skin was furnished with papillæ and protuberances; the intestine had increased in length and was still coiled; the mouth, as in the preceding stages, was placed under the head, at a little distance from the anterior end. Another account states that the horny jaws are not developed. The tail in all embryonic stages was provided with the usual muscles as if for swimming, and was folded against the side of the egg. Wyman shows that, after the supply of gelatinous substance around the egg has been exhausted, the tadpole still continues to increase in size, and he concludes that it must therefore grow at the expense of material from the mother, probably by a secretion of the wall of the cell. In summing up the development of Pipa, Wyman notes that the embryo goes through the usual metamorphosis, having internal and external gills and lungs, also a tail adapted to swimming, although the gills and tail are never used as in the frog. The external branchiæ are lost at a very early period, and the tail is absorbed before the animal escapes from the back of the parent.

The folds of skin covering the internal gills differ from the operculum of the frog in that they open on both sides, and the anterior legs are not covered by them. These relations are similar to those in the larva of Dactylethra, the other representative of the primitive suborder of Aglossa. The presence of external gills has been doubted at various times, but the balance of evidence and the last word on the subject seem to show that they exist for a short period.

An early writer, according to subsequent quotations, affirmed that the tail is devoid of pigment, and believed that it is an embryonic breathing organ. This idea was entertained at a time when the presence of gills was not known; it is not in accordance with Wyman's account, nor with Spallanzani's (**1785**), who concluded, after a careful examination, that the tail does not differ from that of the ordinary tadpole. Furthermore,

Bronn and Balfour state that the tail is absorbed before hatching, and Bronn has implied, as already mentioned, that the hatched young remain for a time on the parent's back. If these statements be true, and if it were also true that the tail assumes the function of respiration, then the animal would be deprived of the embryonic breathing organ some time before it escapes from the cell on the parent's back.

Alytes obstetricans[1] is unique among European frogs in not laying its eggs in water. It occurs in various parts of Europe, such as the Rhine region in Germany, the neighborhood of Marbourg, Paris, and Liège. It has been said that it lives only in regions of hilly ground, where there are clear springs; but Cope ('**85**) records that it is common in dry places near Berlin. The frog digs skillfully, and remains underground by day, but at night it is active in the search for food.

The eggs are laid from March to June (according to locality), in a double string of gelatinous substance. The male loops the eggs about its hind legs in the form of a figure 8, and thus carries them, for about three weeks, when the young have reached a stage of development far beyond that of the typical tadpole at the time of hatching. At the end of the period the male takes the eggs to water, and there the tadpoles leave the egg-membrane, and at once swim about actively. They are said to winter in the tadpole stage, although Claus ('**66**) has affirmed that the metamorphosis is completed in a month. When the tadpole leaves the egg, the external gills are already reduced, and the internal gills are fully developed; the opercular opening is median; the tail is ready for swimming; the lungs are developed; the horny jaws, teeth, and fringed lips are formed (these are said to appear later than in the ordinary frog); the intestine is coiled, and the liver is present; the head kidney is in process of degeneration, and the mesonephros partially developed; the legs are not formed. It has been suggested that the lungs are used before hatching, because air bubbles are given off as soon as the tadpoles reach the water.

[1] A complete account of Vogt's ('**42**) article is not given here. Gasser ('**82**) also describes details not mentioned here, especially in regard to the blastopore, the germ layers, and the development of the pronephros and kidneys.

The egg contains an unusual amount of yolk, and is not pigmented; the segmentation was formerly thought to be meroblastic, but it has recently been described as similar to that of Bombinator. The embryo is said to be ciliated even on the head. Certain peculiarities in the development of the alimentary canal have been recorded. The cavity is at first wide, and in the foregut and hindgut it remains in this condition, the anterior end having the widest lumen; in the middle region the ventral yolk-mass is raised in a ridge, toward the dorsal wall, so that the midgut is, for a time, nearly or entirely barricaded. An early description seems to indicate that the œsophagus is at one time closed by yolk-cells, as in the frog. The liver is said to develop independently, and shortly to acquire an opening into the alimentary canal. It is also said that the vitelline veins are at first not connected with the liver, but pass into it later as the portal vein. The lungs arise as solid masses of cells in the œsophageal region, and subsequently become hollow. An adhesive gland is not mentioned.

Before the gills develop, four gill-slits break through; the external gills are then represented by a single pair, on the third visceral arch; they grow to an unusual length during the life in the egg, and are branched eight or ten times. These delicate plumes are very highly vascular and therefore bright red, and are easily seen through the egg-membrane.

When the tadpoles are about ready to leave the egg, the hatching may be hastened or retarded within the limits of two or three days, by bringing the eggs into water a little before or after the normal time. Tadpoles that were put into water long before the usual time, for example when the external gills were fully developed, fruitlessly turned within the egg-membrane, and finally died.[1] On the other hand, Agassiz tried without success the converse experiment of raising the newly hatched young in air.

Some interesting facts have been discovered in connection

[1] The experiment of first cutting away the egg-membrane and then leaving the tadpoles in water was apparently not tried. Compare experiments on the embryos of the viviparous *Salamandra atra*. Those taken from the uterus, if tended with great care, cast off their gills in water and develop a new set. Chauvin ('**77**).

with the Venezuelan frog *Nototrema oviferum* (*Notodelphys ovipara, Opisthodelphys oviferum*), found at Puerto Cabello. The female is provided with a large dorsal pouch, which opens to the outside at its posterior end. It has been regarded as an invagination of the skin, and unlike the dorsal cells of Pipa it is a permanent organ. Weinland ('54) has described fifteen embryos that were contained in the pouch of one specimen, and had all reached the same point in development. They measured 18 mm. from head to tail, and were folded over a large yolk-mass, that formed about seven-eighths of the egg. The embryos were dark with pigment, but over the yolk there were only scattered pigment cells. The rudiments of body muscles are described as present beneath the skin about the yolk. The head was well defined and of the shape peculiar to the adult, with prominent eyes and semicircular nasal openings. The mouth was ventral near the anterior edge of the head, and measured little less than one-half the width of the head. It is said in the course of the description that the horny jaws were not developed, although at another place in the same account the embryo is paralleled, in respect to the mouth, with the newly hatched Alytes, where the tadpole mouth-parts are present.

In the embryo of Nototrema no adhesive gland was found, and the tongue was not developed. The fore legs measured about 2 mm. and were concealed beneath the operculum; the hind legs were twice as long, the toes were forming. The tail measured 5 mm. in length and 2 mm. in width, and with the hind legs was laid against the side of the egg. The heart was three-chambered, and the aortic arches separated not far from it. The dorsal aorta, posterior vena cava, and portal vein from the gut to the liver were large vessels. The lungs were well developed. The three-lobed liver, the gall bladder, and large pancreas were present, the pancreas surrounded by a coil of gut, leading to the stomach portion. The foregut and also the hindgut were thick-walled and appeared white, while the gut between them was formed of coils packed with yellow yolk. The pronephros had entirely disappeared, and the fat bodies and the kidneys were present.

The most remarkable structures were the gills. Three visceral arches were present, and according to one statement three gill-slits (three slits appear in the figures, but in another part of the description it is said that the first and third arches have each only one free edge — a condition that would admit of only two slits). The gills consisted of a pair of very thin bell-shaped membranes, each gill connected with the gill arches by two filaments, one ending on the first and one on the second arch. This peculiar arrangement led Weinland to the conclusion that the bells represent two gills fused together. He regarded them, in function at least, as external gills. On the free edge of the third arch was found the rudiment of what was supposed to be an internal gill, which suggested that the bell-gills are temporary larval organs. The bell-gills were veined by a capillary network, and the vessels were filled with blood, so that the gills were probably already functioning, although pressed close to the embryo in the egg; it was only after floating them out in water that their windflower shape and large size were discovered. The gill measured across, when expanded, not less than three-quarters of the diameter of the egg. The gill filaments were provided with striped muscle fibres; these muscles, Weinland argued, could not be of use in the egg, but the gills may be retained a short time after hatching, when the muscles might function in water, whether the tadpole remained within the pouch or escaped.

Weinland knew nothing of the subsequent history of the tadpoles, as to when they hatch and whether they ever live in water, either free or within the pouch; Boulenger makes some unqualified statements in regard to these questions.

He has noted the occurrence of eggs in the dorsal pouch of the female of *Nototrema fissipes;* he observed a single specimen, in which there were sixteen ova, measuring each 10 mm. in diameter. "From the size and small number of the ova," he writes, "it may be safely predicted that the young undergo the whole of the metamorphosis, within the pouch, as in *Nototrema oviferum*, which is the nearest ally of *Nototrema fissipes.*" Of two species of Nototrema found in Ecuador and Peru, also provided with pouches, Boulenger says in an earlier work ('82),

"In *Nototrema testitudineum*, as in *Nototrema oviferum*, the young undergo their complete metamorphosis in the maternal pouch; while in *Nototrema marsupiatum* they leave the pouch in the tadpole state." The tadpoles of *Nototrema marsupiatum*, and those of another species, *Nototrema plumbeum*, are set free in water, according to Werner ('98).

Yet another frog of the tropical Andes, *Amphignathodon güntheri*, is said to have a dorsal pouch, which is probably a receptacle for eggs.

The female of a small Venezuelan species, *Nototrema pygmæum*, bears from four to seven young in a dorsal pouch, which splits open when the development of the tadpoles is complete. The pressure of the active young starts the splitting of the pouch at the slit-shaped posterior opening, and the whole pouch is laid open in the middle line. The pocket is perhaps formed from lateral folds after the eggs are placed on the back, and is possibly not closed again after the young escape, but is formed anew at the next breeding season; or the pouch is perhaps never formed a second time.

Observations on a number of tadpoles of *Rhinoderma darwinii* have disclosed some of the facts of the development of this interesting frog. It was first discovered on the voyage of the *Beagle*, in the shady forest of the province of Valdiera in Chile. It was formerly supposed to be oviparous, but, in reality, the tadpoles develop in an enormously expanded gular pouch, which covers nearly the entire ventral side of the male frog.

One account tells of fifty embryos in the pouches of five adults, and a much later account describes certain features of eleven tadpoles of one pouch. The tadpoles from one adult are not equally developed.

The youngest tadpoles described were thought to be just hatched. They measured 4 mm. to the tail; the alimentary canal was not differentiated, but contained much yolk. In all later specimens the alimentary canal was short, coiled, and of a yellow color, due to the presence of yolk. No external gills were observed, nor horny mouth-parts. Internal gills are not mentioned, although the anterior legs in young stages are concealed beneath a fold of skin (suggesting the operculum).

The hind legs develop before the fore legs and in late stages the feet are webbed. The tail is weak and small, and in the youngest embryos lies along the middle line of the egg-sphere. The oldest tadpoles had lost the tail, but at a period before its absorption both fore and hind legs were present and free.

The adults of *Hyla gœldii* have been found in Rio de Janeiro in water, contained in the central cup of certain Bromeliaceæ, and also on dry bamboo near Bromelia. The dorsal skin of the female is slightly raised around the edge of the back, forming a shallow cup, where the eggs are carried. In one case the dorsal vessel contained twenty-six pale eggs. Judging from the figures, the embryos, in external appearance, resemble to a remarkable degree those of *Hylodes martinicensis*. They are unpigmented and are bent around a large yolk-mass, 4 mm. in diameter. The head, which is large and flat, and the eyes may be seen through the egg-membrane. No traces of gills were discovered. The accounts vary as to the condition of the embryo when hatched. According to Goeldi ('95), frogs that hatched in confinement possessed both pairs of legs and small tails; the young jumped about actively and preferred not to stay in water. No details are recorded, but it is implied that the development is abridged and direct. Werner ('98) affirms that the tadpoles are ready to swim when hatched, and that the mother finds water to deposit them in. According to Fritz Müller's description in a letter to Darwin, the tadpole which he observed did not possess fore legs until two weeks after hatching; he saw no external branchiæ or opening that might lead to internal branchiæ.

Another mode of carrying eggs by the female frog is seen in the case of *Rhacophorus reticulatus* (*Polypedates reticulatus*). A single specimen, which was captured at a high elevation in Ceylon, carried twenty-one ova adhering firmly to the abdomen. It is uncertain whether the frog was caught in water or on land, and nothing has been noted as to the development.

An interesting adaptation in a dry climate is recorded of a species of *Spea* (*hammondii?*) in western North America. The eggs are deposited in rain pools, which collect in the dry arroyas and in the low lands. The tadpoles acquire their legs

very early, and are soon able to escape from the muddy fluid; thus, by accelerated metamorphosis, the chances of succumbing because of drought are lessened.

Lythodites latrans, which lives in fissures of limestone precipices of western Texas, is also supposed to deposit its eggs in pools of rain water.

The eggs of *Phryniscus nigricans*, in Paraguay, are laid singly, in temporary pools in grassy ground. "The eggs and larvæ do not seem to differ in any great degree from those of Rana. There is, however, a very large yolk plug, which remains evident after the closure of the neural groove." The development is very rapid, and, within twenty-four hours after segmentation begins, the tadpoles are hatched and wriggling about. They are probably washed into deeper pools.

Another case of rapid development is that of *Paludicola fuscomaculata*, also found in Paraguay. It spawns in January in shallow pools, and the eggs float on the surface. They measure 1 mm., are unpigmented, and have very little yolk. The tadpoles hatch within eighteen to twenty-four hours after segmentation begins, and hang in the water from the floating froth. "Many of the processes of development are blurred and, as it were, hurried over. The external gills never reach a high state of development."

Eggs which are thought to develop like those of Paludicola are said by the natives of Paraguay to belong to the frog called by them "Po it," more scientifically *Eugystoma ovale*. Eggs and larvæ are found in froth in holes in the ground, beneath fallen tree trunks. The nests "were a most ingenious contrivance for collecting water and keeping the eggs and larvæ at least moist between the storms of the wet season. They were always found within the forest belts which lay on the highest ground." The larvæ "would exist for a very long time in a small quantity of water without increasing in size, but when removed to a tank they grew enormously and very soon left the water."

A curious indifference to water has been observed in the case of *Spea bombifrons*, near Market Lake, in Idaho. The tadpoles, still "in the free-swimming condition," but entirely

air-breathers, were seen quite out of reach of the water, in small spaces which they had cleared in the ground. The legs were full-grown, the tail undiminished, the jaws toothless and cartilaginous and "some quite larval in form."

Two species of Dendrobates resort to a device by which it is supposed that the young are transferred from one pool to another. The accounts are sometimes referred to as if they related to a single species. The species closely resemble each other, except in size; the larger, *Dendrobates trivittatus*,[1] is found in Dutch Guiana, the smaller, *Dendrobates braccatus*,[2] occurs in western Brazil. These frogs and *Phyllobates trinitatus* from Trinidad and Venezuela have the habit of carrying their tadpoles attached to the back, whether by suckers or by a viscid secretion from the parent, or by both, has not been determined. It has been observed in the case of *D. trivittatus* that the frog spawns in water, and that the free-swimming tadpoles attach themselves to the parent. They adhere firmly, since they were not brushed off when the parent was hotly pursued and crawled rapidly through the grass; the frog on this occasion was found far from water, and emerged from the grass and bushes freshly wet with rain.

D. braccatus is found on a table-land where, even in the wet season, the water may dry off in two or three days.

The tadpoles of both species possess the usual larval organs, including the horny mouth-parts. The intestine of the tadpole of *D. trivittatus* is said to be shorter and less coiled than in the ordinary tadpole, and to contain yolk.

In the case of Phyllobates it is the male frog that transports the young, but the sex of the frog is not recorded in either case of Dendrobates. The tadpoles of Phyllobates are ranoid, and the tail is about twice as long as the body; the anus is dextral, and the spiraculum sinistral.

[1] *Dendrobates trivittatus* has been wrongly called by one observer (Wyman, '59) *Hylodes lineatus*.

[2] Smith, in describing *Dendrobates braccatus*, reports that the natives of Brazil brought him from the Santarem forest a similar, though larger, frog and affirmed that, like *Dendrobates braccatus*, it transports its young. This may have been *Dendrobates trivittatus*, which is described by Wyman and others, since the difference between the two species is one of size.

A case which resembles Phyllobates and the like, superficially at least, has been discovered by Brauer ('98) in the Seychelles. *Arthroleptis seychellensis* inhabits a forest about 500 feet above the sea, where the streams are swift and there is no still water. The frogs are found in decayed trunks and among damp leaves on the ground, and on one occasion, late in August, a number of eggs were found under leaves from which the adult had been frightened away. The eggs were not included in a common gelatinous covering; they hatched in a glass, and the tadpoles immediately stuck to the glass by their abdomens. Tadpoles of about the same stage of development were also found adhering to the back and sides of an adult. The tadpoles had prominent eyes, mouth well under the anterior end of the head, short hind legs, fore legs concealed beneath an operculum, rudder tails more than twice as long as the body, and a large amount of yolk bulging out on either side of the body. No opening was found to the operculum, and no internal gills, nor were the rudiments of lungs discovered. The outer layer of epithelial cells on the abdomen was columnar, making the epithelium appreciably thicker there than elsewhere; gland cells were wanting on the abdomen only, though a slimy secretion covered the surface. An adult carrying older tadpoles was found at another time. Gland cells were present on the abdomens of these tadpoles; the anterior legs had come through the skin, the toes were found on all the feet, the length of the tail was not reduced in proportion to the body, and much yolk was still present. Rudiments of lungs were found, and the entodermic epithelium had differentiated from the yolk.

Brauer concludes that the eggs are covered with leaves by the parent (probably the male), that the young, when hatched, place themselves, with the assistance of their tails, on the parent's back, where they adhere partly by suction, partly by aid of the roughness of the parent's skin, and partly by a secretion, largely from the adult. Finally, the tadpoles are not attached to the parent for transportation to water, but undergo a large part of their development on its back.

Hylodes martinicensis has been described as the "coqui"

found on several of the islands of the West Indies. Superficial descriptions of the eggs are recorded by two writers (Bello, '71; Peters, '76). The eggs were found on damp leaves of plants, and near them was the female, apparently on guard. The frogs hatched in the adult form after fourteen days. The embryo is described as wrapped about the yolk, like a mammal. On the seventh or eighth day both pairs of legs were present, and the tail, eyes, and pulsating blood vessels were observed. On the twelfth the characteristic toes and suckers had appeared. The tail was turned downward, with the broad surface pressed against either the right or left side of the embryo. There was no trace of gills or gill-slits, but the tail was so fully supplied with blood that it was regarded, without doubt, as a breathing organ. On the fourteenth day newly hatched embryos were 5 mm. in length, and the tail, which measured about 1.8 mm., was absorbed during the course of the day.

In 1873 there appeared in several magazines various accounts, by Bavay, of a frog which he called *Hylodes martinicensis*. The accounts differ in some respects from those of the other observers of Hylodes, but are not altogether consistent among themselves, so that Bavay's observations were probably not very accurate. He affirms that in one locality, at least, spawning does not take place during the dry season, or even after lack of rain in the wet season; the eggs are always found in damp places, under stones or with decaying leaves. Instead of fourteen days, he allows only ten or eleven for hatching, and states that the frog goes through the usual metamorphosis within the egg. The eyes, legs, tail, and feet he describes at a period earlier than that in which they were found by the other observers, but in regard to the tail his own accounts vary; he stated at first that it disappeared two days before hatching, but afterwards announced in a published letter that he found a vestige of a tail in tadpoles just hatched, when they were hardened in glycerine. The vitellus, according to his observations, was at first connected with the embryo by a cord, for the embryo on the fourth day moved independently of the yolk-mass, although at the same time both

rotated together in the egg. On the sixth day the yolk was covered with a vascular network, and on the ninth it had been incorporated in the body. On the fourth day, when the embryo was turning actively, the heart was beating, and on either side of it there was a trace of a gill; a vein and artery were seen running parallel in the gill. In the course of the next few days the gills had first increased and become blood-red, then diminished, and on the seventh day only a red spot remained, which disappeared on the ninth. Bavay's observations were made in Guadeloupe, and it is possible that on this island there is a frog differing from *Hylodes martinicensis* in the points indicated by Bavay's description.

A study of two stages of the excretory system of Hylodes led Selenka ('82) to the opinion that the embryonic and permanent kidneys develop earlier than in the frog, producing a condition which approaches that of reptiles.

It would be interesting to know something of the development of *Hylella platycephala*, a frog which occurs in southern Mexico. It is said to lay its eggs in the axils of the leaves of Tillandsia, where the frog "undergoes its metamorphosis, high above the ground."[1]

Whether the entire development occurs within the egg-membrane, and whether water continually remains on the plant is not stated.

A short note on a frog, supposed to be *Hylodes lineatus*, records some evidence that its embryos undergo their entire development within the egg-membrane. The eggs have been found in Peru under grass far from water, and the embryo not yet hatched possessed no trace of a tail, but well-developed feet provided with suckers.

The young of *Rana opisthodon* hatch in the adult condition. Eggs were collected in crevices of rocks close to a stream on a peak of one of the Solomon Islands. The eggs measured from 6 to 10 mm. in diameter. In the younger stages the

[1] Andrews ('92) reports that the eggs of a tree frog in Jamaica have been found in the water at the bases of the leaves of epiphytic bromelias. They were observed in early stages of development, at the end of May, in the region of Mandeville.

embryo was folded around a large yolk-mass in the same way as *Hylodes martiniccnsis*. The tail was entirely wanting in the more advanced specimens. No traces of gills were found, but on each side of the body were several transverse folds of skin that were thought to be respiratory organs. The legs were well developed; the anterior were shorter than the posterior. The tip of the upper lip was furnished with a small conical protuberance, which in one case projected through the envelope of the egg, suggesting that its function is to perforate the egg-membrane.

The South African frog *Dactylethra capensis*, like *Pipa americana*, the other representative of the Aglossa, lives entirely in water; the tadpoles of the two forms agree in having the fore limbs free from the operculum and in having two spiraculæ.

Leslie ('90) writes of Dactylethra (called by him Xenopus): "Its habits are essentially aquatic, the animal never leaving the water except in search of places where food or shelter is better supplied. Unlike other frogs, it feeds in the water, on insects, small fishes, or even young and larvæ of its own kind, and is apparently unable to feed out of that element. The mode of eating is by forcing the prey into the mouth by means of the hands, which act as a pair of claspers; the deglutition always takes place under water. Locomotion on land is by difficult and awkward crawling and leaping. But Xenopus is a most admirable swimmer, and remarkable for the manner in which it remains poised for a long time immediately under the surface of the water, with the nostrils only exposed. The whole structure of the animal denotes its thoroughly aquatic habits — the broadly webbed toes, the smooth, slimy skin with its symmetrically disposed muciferous tubules; there are no eyelids proper, but merely the transparent nictitating membrane, moving up and down; and the nostrils have a disk-like internal valve. When at rest, Xenopus never assumes a sitting posture like other frogs and toads, and the back never appears humped."

The eggs (measuring about one-sixteenth inch in diameter) are laid singly and attached to water-plants or stones, each

surrounded by a mucilaginous covering. They are at first very slightly pigmented. Tadpoles in the Zoölogical Gardens in London hatched in about two days; the head of the newly hatched tadpole is broad and flat; the fin is developed on the tail to the posterior end, and there is no chimæroid lash as Parker ('77), and subsequently the text-books, have figured; the intestine is coiled as usual. The tadpoles in confinement had access to vegetable food, but subsisted entirely on an animal diet. A single ventral adhesive gland persists for a long time and at an early period occupies the whole ventral surface of the head. The buccal cavity is open to the exterior the day after hatching. No jaws or beak develop. A few days after hatching a pair of tentacles develop on either side at the angles of the jaw; one of them may become bifurcated and each is provided with two channels through which the blood streams. External gills are not wholly wanting (as was formerly thought), for two days after hatching, when the operculum is commencing as a free fold, there are vascular lamellæ on the first three branchial arches. The gill-slits open later than the mouth; the hyoid cleft opens last by a tube into the first branchial cleft, a long way from its opening to the exterior. At the same time that the gill-slits open, a tufted filtering apparatus is developed from the branchial arches; this becomes vascular and must, it is thought, be respiratory, as no internal gills develop. The opercular folds do not cover the arms, but open by a slit on each side, anterior to the arm. The spiraculæ persist for a long time. The pronephros develops as in the ordinary frog. The vascular system develops as described by Maurer for *Rana esculenta*.

It is evident from the foregoing review that many points in the embryology of the Anura remain to be investigated; it is not, however, surprising that the work has been left undone, when we consider the geographical, the climatic, and other difficulties attendant upon making observations and collecting material.

GERMANTOWN, PENN., 1900.

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APPENDIX I.

Since this paper went to press, there have appeared the following notes on Nototrema by Brandes, '99. "Larven zweier Nototrema-Arten. Demonstration." *Verhandlung der deutschen Zool. Ges., 9. Jahresvers.* Hamburg, p. 288.

The female of *Nototrema marsupiatum* carries a great number of small eggs (200). The full-grown larva has a rudder-tail with a well developed capillary network, hind legs in the condition of knobs, horny teeth, and an operculum with a lateral spiraculum. Through the spiraculum project two filaments, which can be traced to the first and second gill arches of the opposite side. The filaments are expanded at their ends into a delicate membrane, spread out under the egg-membrane. The gills are thus reduced to two, both arising from the same side. In the larva examined, the yolk had been entirely absorbed, so that life in the egg-membrane was no longer possible. A larva caught in water resembled a tadpole of the European Pelobates shortly before metamorphosis.

Nototrema oviferum carries only thirty large eggs. The tadpoles observed had well developed hind legs; the tails had entirely degenerated; there was no spiraculum, but through a broad slit in the operculum projected the two bell-gills described by Weinland ('54a). Four gill arches were present, and the gill filaments were attached to the first and second arches.

APPENDIX II.

Index to species, with a summary of references to each.

Nototrema oviferum (*Notodelphys oviferum*. *Opisthodelphys oviferum*). Venezuela.
Weinland, '54a. *Ib.*, '54b. Berthold, '56. Wyman, '57. *Ib.*, '59. Owen, '66. De l'Isle, '76. Nature, '77. Bronn, '78. Boulenger, '82. Cope, '85. Howes, '88. Sarasin, '87. Boulenger, '86a. Page **698**.

Nototrema plumbeum.
Werner, '98. Page **700**.

Nototrema pygmæum. Puerto Cabella, Venezuela.
Werner, '98. Page **700**.

Nototrema testitudineum. Ecuador. Peru.
Boulenger, '82. Cope, '85. Sarasin, '87. Boulenger, '86a. Page **700**.

Paludicola fuscomaculata. Paraguay.
Budgett, '99. Page **702**.

Phryniscus nigricans. Paraguay.
Budgett, '99. Page **702**.

Phyllobates trinitatus. Trinidad. Venezuela.
Boulenger, '95. Werner, '98. Page **703**.

Phyllomedusa hypochondrialis. Paraguay.
Budgett, '99. Page **690**.

Phyllomedusa iheringii. Rio Grande.
Ihering, '86. Knauer, '78. Howes, '88. Sarasin, '87. Goeldi, '95. Werner, '98. Page **690**.

Pipa americana. British and Dutch Guiana.
Fermin, 1765a. *Ib.*, 1765b. Laurenti, 1768. Göze, 1776. Spallanzani, 1785. Camper, 1788. Wyman, '54a. *Ib.*, '54b. Parker, '77. Wilder, '77. Sclater, '95. Leydig, '96. Bartlett, '96. Duméril et Bibron, '54. Wyman, '57. Peters, '76. Nature, '77. Knauer, '78. Bronn, '78. Boulenger, '86a. Schönichen, '97. Werner, '98. Page **693**.

Polypedates maculatus. Ceylon.
Gunther, '76. Ferguson, '76. Sarasin, '87. Page **693**.

Rana opisthodon. Solomon Islands.
Boulenger, '86b. Sarasin, '87. Boulenger, '86a. Page **706**.

Rana temporalis. Ceylon.
Sarasin, '87. Page **693**.

Rhacophorus eques. Ceylon.
Sarasin, '87. Page **691**.

Rhacophorus reticulatus (*Polypedates reticulatus*). Ceylon.
Günther, '76. Ferguson, '76. Bronn, '78. Boulenger, '86a. Page **701**.

Rhacophorus schlegelii. Japan.
Holland, '89. Ikeda, '97. Werner, '98. Page **689**.

Rhinoderma darwinii. Chile.
Gay, '36. Espada, '72. Spengel, '77. Howes, '88. Bronn, '78. Boulenger, '86a. Plate, '97. Werner, '98. Page **700**.

Spea bombifrons. Idaho.
Cope, '85. Page **702**.

Spea hammondii. Western North America.
Cope, '85. Page **701**.